

# FLORAL EVOLUTION IN *VIOLA*

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## ABSTRACT

Pollination in *Viola* results both from sternotribic and nototribic pollinator responses, the frequencies of which vary according to the plant species. Syndromes of floral characters determine these frequencies, and each is adaptive to a group of pollinators, of variable taxonomic heterogeneity, characterised by particular morphology and behavior. Some syndromes elicit equal frequencies of sterno- and nototribic responses, while others elicit chiefly, or exclusively, one type, and coevolution with a single insect genus may be in progress. One effect of the differing syndromes is the partitioning of pollinator resources among simultaneously flowering species.

An evolutionary sequence for the floral syndromes is proposed which, in broad agreement with systematic conclusions, considers yellow-flowered, sternotribic *Chamaemelum* violets as the most ancient and blue-flowered sterno- or nototribic violets of the sections *Rostellatae* and *Plagiostigma* as the most recently evolved. Species of the section *Melanium* (the pansies), in which cleistogamy is almost absent, appear to be an early offshoot leading to multicolored, nototribic flowers.

The "generalist" syndromes were probably vital to the success of the genus in (a) invading the northern and southern temperate zones and (b) adapting to widespread habitat disturbance by man. The basic structure of the violet flower is adaptive to a temperate pollinator complex to be found over very large geographic areas. Floral variations demonstrate adaptive radiation to many ecological conditions.

One of the interesting fields remaining in pollination biology is the creation of a synthetic theory of evolution that links the processes of differentiation of pollination systems as observed in living plant populations with the major trends of coevolution over very long periods of time. The evolution of pollination systems in individual angiosperm families has been the subject of several elegant studies such as Lewis and Raven (1961), Grant and Grant (1965), and Eyde and Morgan (1973). In most cases the sequential stages in evolution have been typological; the data indicating only major changes in mode of pollination from one group of animals to another, for example from insects to birds. The actual processes of differentiation are still very poorly understood. The purpose of this paper is to suggest processes of change in the pollination systems of *Viola* and then to examine their operation both from contemporary and historical perspectives. Therefore, discussion will focus first on data from living populations and second on how this data may be applied to a phylogeny of pollination systems in the genus.

## THE POLLINATION MECHANISM: CLASSICAL DESCRIPTION

This may be best described with reference to Figures 1 and 2. The proboscis of the pollinator, loaded with pollen from another flower, is inserted into the petal-spur via the furrow in the anterior petal. As the proboscis and adjacent structures slide under the style the pollen load accumulates at the opening of the stigmatic cavity, which acts as a scoop, like a snow-shovel. Simple extension of the proboscis is insufficient to obtain nectar so the head of the insect is pushed

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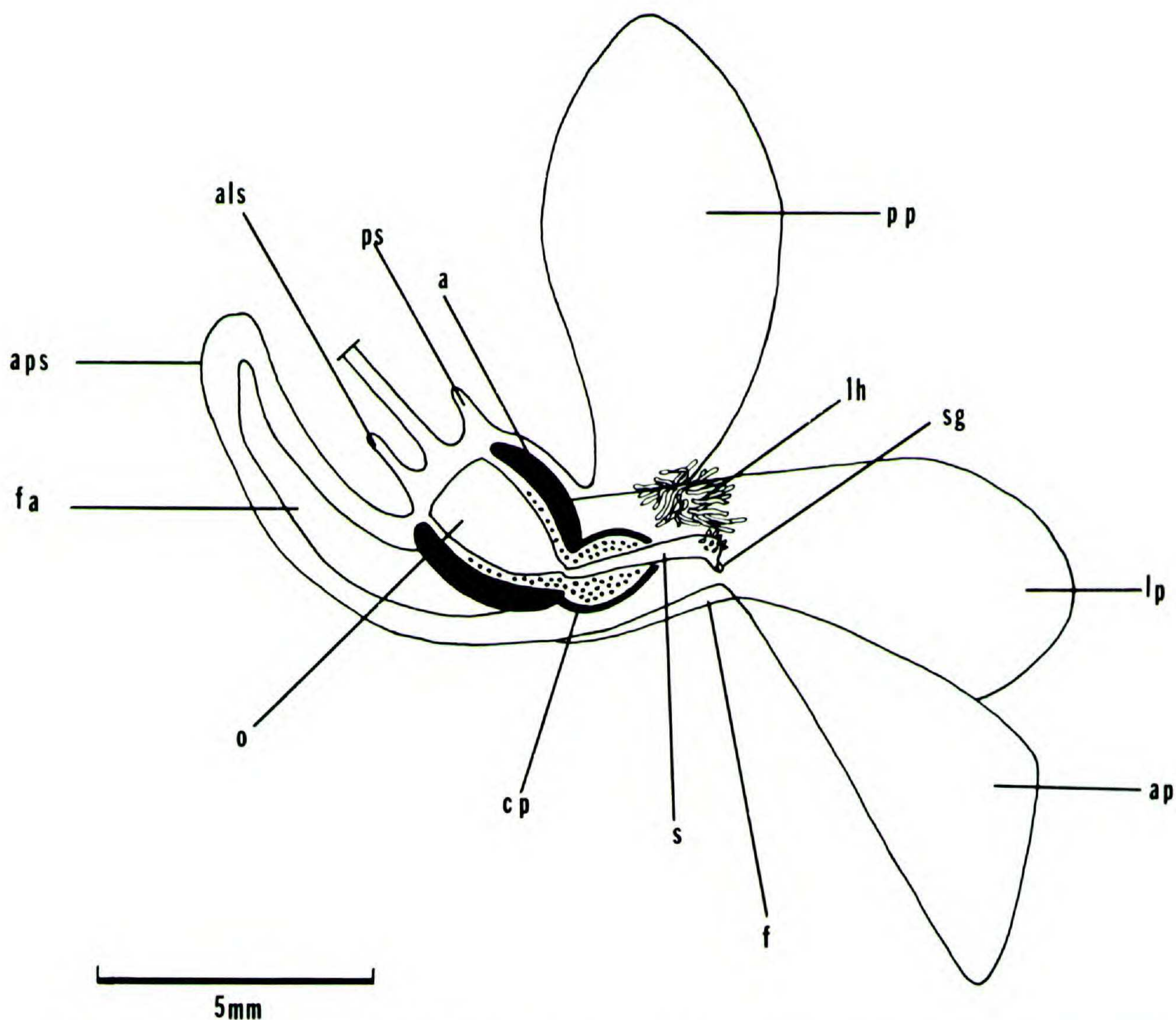


FIGURE 1. Diagrammatic half-flower of *Viola*. als: anterior sepal, ap: anterior petal, aps: anterior petal-spur, a: anther, cp: connective appendage, f: furrow in anterior petal, fa: filament appendage (nectary), lh: lateral hairs ("beards"), lp: lateral petal, o: ovary, pp: posterior petal, ps: posterior sepal, s: style, sg: opening of stigmatic cavity.

into the flower, below the style, raising it to a steep angle. This deflection acts as a lever to open the cone of connective appendages which contains the loose, powdery pollen. It is this opening in the appendages through which a new load of pollen cascades on to the pollinator, normally the dorsal surfaces of the proboscis and head. Simultaneously the old pollen load at the stigma-opening is pushed into the stigmatic cavity by the head of the pollinator. When the proboscis is withdrawn the style snaps back into place, closing the cone of appendages and, by a kind of suction, ingesting any pollen still remaining outside the stigmatic cavity. Figure 2 shows clearly that the classical view is that *Viola* is nototribe and adapted to long- and medium-tongued, nectar-seeking insects—especially bees.

#### THE POLLINATION MECHANISM: REVISED DESCRIPTION

It is curious that the great classical pollination biologist Christian Sprengel, having described the above mechanism, provided an illustration of a bee feeding in a completely different posture. And it is a fact that a large proportion of in-

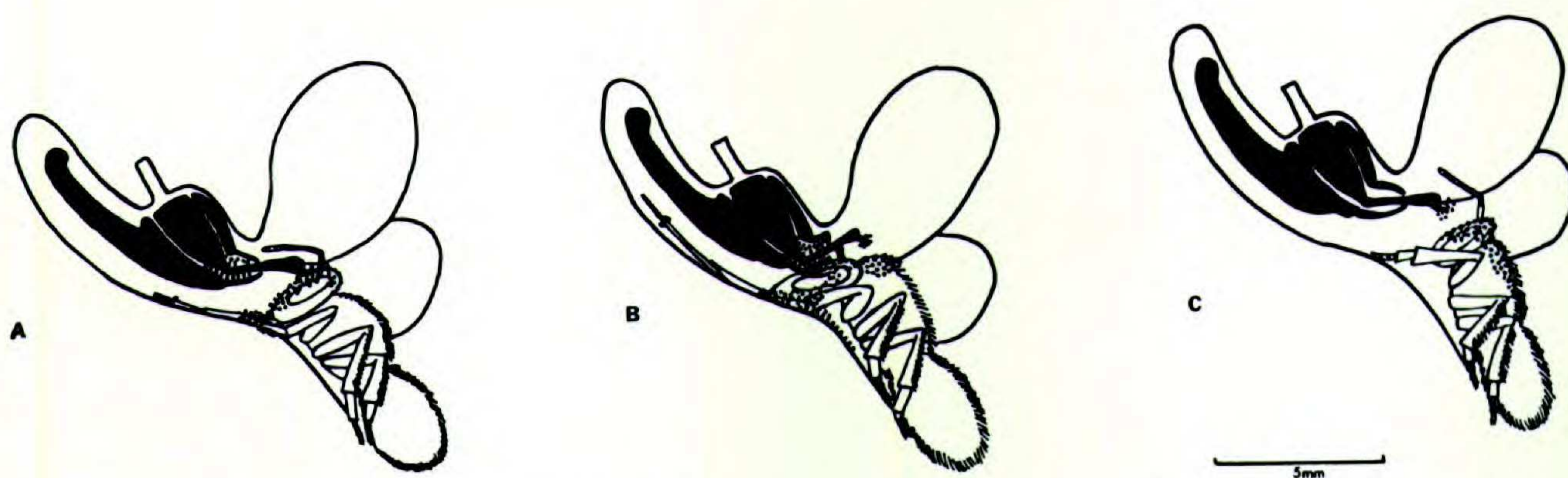


FIGURE 2. Diagram to show nototribic pollination in *Viola*.—A. Proboscis inserted into petal spur; pollen from another flower contacts opening of stigmatic cavity.—B. Proboscis penetrates to nectar; style raised and pollen released.—C. Proboscis withdrawn with new pollen load, style back to resting position.

sect visits involve not the "normal" or prone position as described, but the "upside-down" or supine position illustrated by Figure 3. Most solitary bees adopt the supine position while feeding. Usually the insect orients to the flower as before but prior to probing and feeding rotates so as to be virtually standing on its head. It can be seen from Figure 3 that the pollination mechanism operates exactly as before but *the flower is now sternotribe*. A further difference is that more of the insect receives pollen, it usually being scattered over the ventral surfaces of the proboscis, head, and thorax. Even the ventral abdomen becomes involved in bees with abdominal pollen scopae. Also the solitary bees which operate the pollination mechanism by the supine feeding position are frequently seeking, and getting, both nectar and pollen. A complete description of all the mechanisms and positions may be found in Beattie (1971).

#### STERNOTRIBY VERSUS NOTOTRIBY

All species of *Viola* so far investigated in the field experience pollination by several groups of insects and are said to exhibit a spectrum of pollinators and pollination effects. Thus, medium- and long-tongued, nectar-seeking insects tend

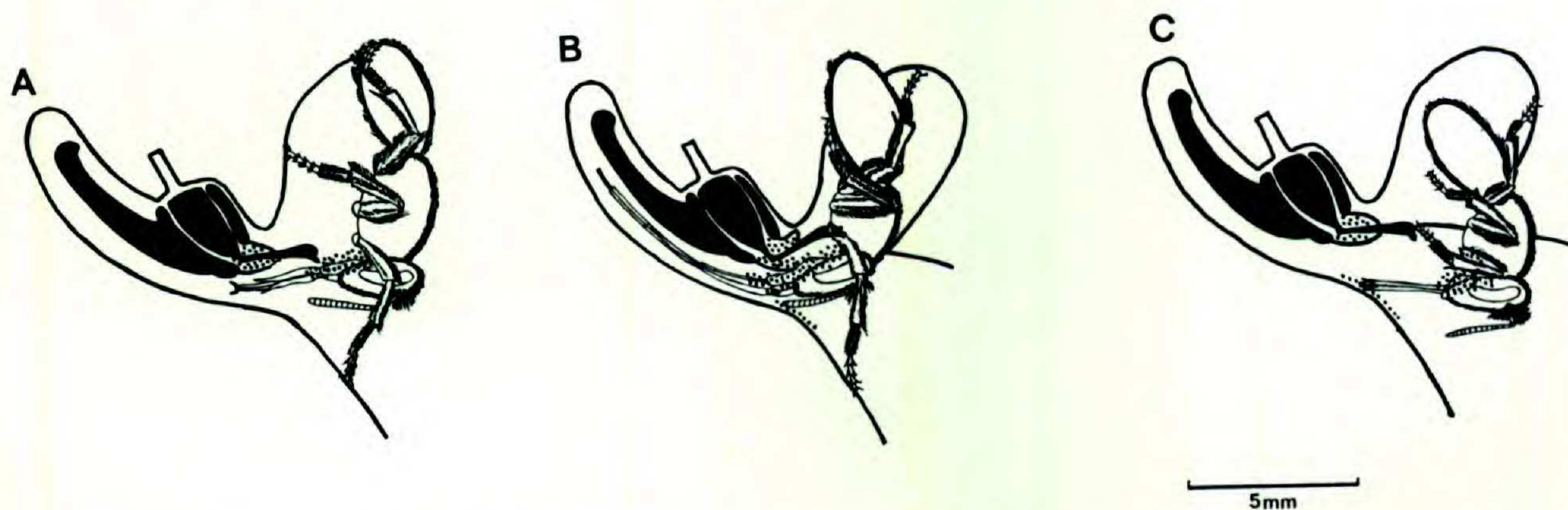


FIGURE 3. Diagram to show sternotribic pollination in *Viola*.—A. Proboscis inserted into petal spur; pollen from another flower contacts opening of stigmatic cavity.—B. Proboscis penetrates to nectar; style raised and pollen released.—C. Proboscis withdrawn with new pollen load, style back to resting position.

TABLE 1. Frequency of visits by bumblebees, solitary bees, syrphids, Bombyliids and Lepidopterans to each of twelve species of *Viola*; expressed as percentage of total number of visits taken from five populations of each species. \*\* = major group of pollinators, 20% or more of total visits. \* = minor group of pollinators, 10-20% of total visits only. (Data for *Viola tricolor* taken from published lists.)

Visitor Species	Viola Species											
	<i>nuttallii</i>	<i>eriocarpa</i>	<i>striata</i>	<i>reichenbachiana</i>	<i>rostrata</i>	<i>hirta</i>	<i>adunca</i>	<i>blanda</i>	<i>papilionacea</i>	<i>fimbriatula</i>	<i>pedata</i>	<i>tricolor</i>
Bumblebees	0	0	19*	19*	0.5	40**	0	0	5	5	10*	93**
Solitary bees	84**	85**	50**	3	28**	40**	89**	87**	64**	95**	64**	0
Syrphids	3	8	28**	70**	15*	0	5.5	8	17*	0	4	0
Bombyliids	1	6	1	8	55**	20**	5.5	5	12	0	1	0
Lepidoptera	12*	1	2	0	1.5	0	0	0	2	0	21**	7
Sternotriby	84	85	50	3	28	40	89	87	64	95	64	0
Nototriby	16	15	50	97	72	60	11	13	36	5	36	100

to be systematic cross-pollinators, while short-tongued or pollen-gathering species tend to be chance cross- or self-pollinators. A glance at Table 1 will show that some violet species receive a majority of visits from just one or two groups (or "bands") of the spectrum, while others receive visits from several. For example, the major pollinators of *Viola nuttallii* are solitary bees, but butterflies may be occasionally important. *Viola striata*, on the other hand, may experience high frequencies of pollination visits by three insect groups: bumblebees, solitary bees, and syrphid flies.

As a consequence of the presence of variable pollination spectra most violet species receive a majority of visits from either sternotribic or nototribic pollinators. The data in Table 1 have been accumulated from prolonged observations of at least five populations of each species; the populations having been chosen on the basis of maximum ecological and geographic differences. Further data has not significantly altered the figures for percentage sternotriby,<sup>2</sup> consequently individual violet species can be characterized as being predominantly sternotribic, predominantly nototribic, or "generalist" (having approximately equal number of the two types of visits).

It is clear from pollination data published elsewhere (*e.g.* Beattie, 1972) that the habitat determines which groups of pollinators may be available to any violet species, and, therefore, habitat preferences exhibited by the plant species will determine to a great extent, the availability of sternotribic and nototribic pollinators. However, certain floral characters do have selective effects in *Viola* and inhibit visits from some groups while encouraging visits from others. Expressing this in more specific terms; the floral biology of individual species may be most adaptive to either sternotribic or to nototribic pollinators, with some intermediates. An interesting consequence of this is the partial partitioning of pollinator resources among sympatric, simultaneously flowering species. For example, *Viola striata* and *V. papilionacea* very frequently bloom together, but *V. striata* is clearly a generalist, while *V. papilionacea* is more sternotribic. The partitioning is clearer between *V. rostrata*, which is nototribic, and *V. blanda*, which is sternotribic. These two species occur together in dense stands in the mesic forests of the Eastern U.S.A., and the assortative foraging of pollinators is easily observable.

#### FLORAL SYNDROMES

The fact that pollinators discriminate between resource species on the basis of obvious differences in the flowers—such as corolla color—has been appreciated by many workers (*e.g.* Levin, 1972). Discrimination of floral characters leading to sternotribic or nototribic visits appears to have a more subtle basis. With the exception of very occasional worker bumblebees, solitary bees are the only

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<sup>2</sup> By contrast with Grant and Grant (1965) there was no evidence for ecogeographical races where the same species is pollinated by different insect groups in different regions. For example, an altitudinal transect across the southwestern Rockies showed that *Viola nuttallii* was visited chiefly by solitary bees wherever it grew, with no increase in fly visitors according to altitude.

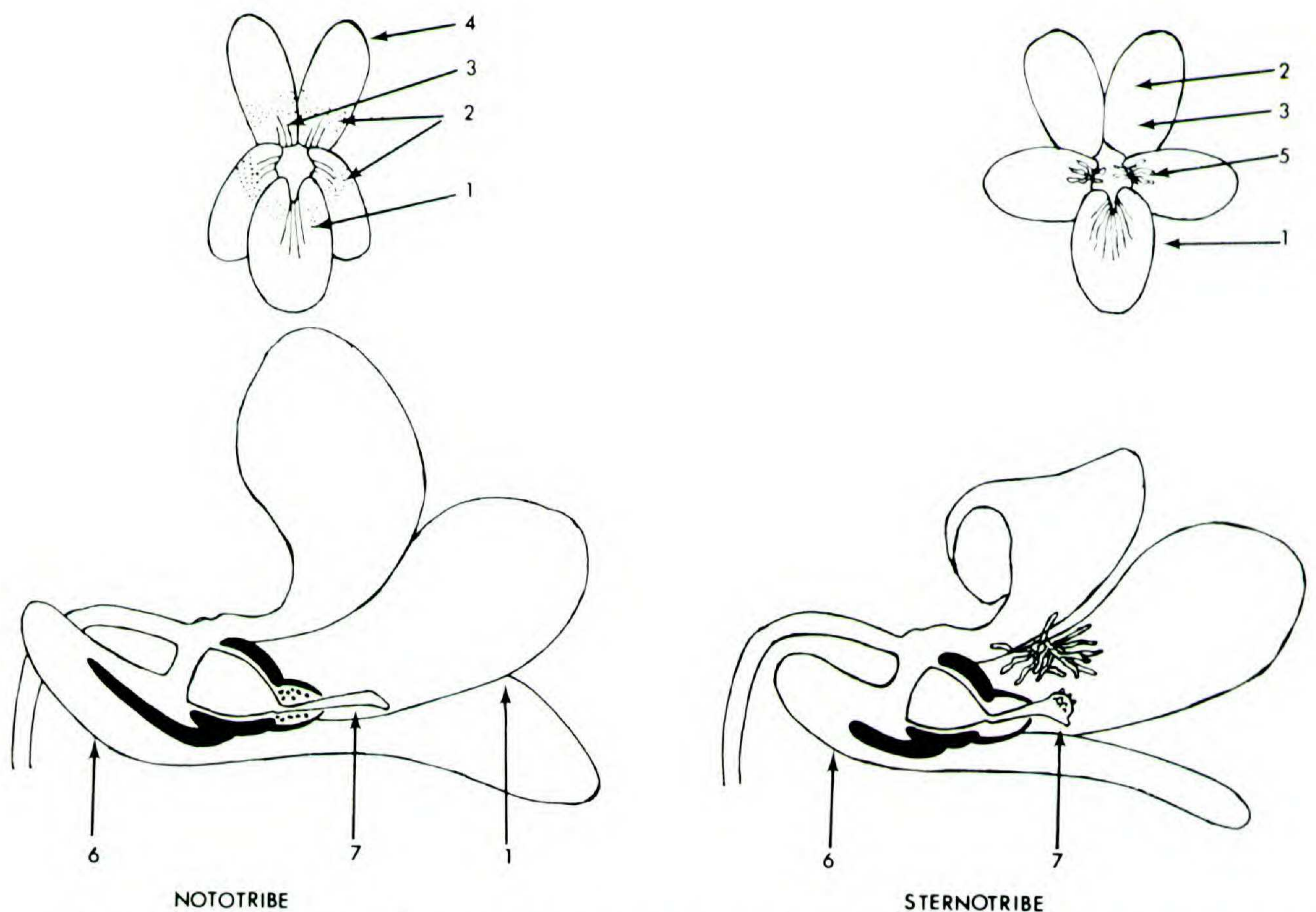


FIGURE 4. Characters of nototribe and sternotribe floral syndromes. For explanation see Table 2.

pollinators which visit sternotribically. Therefore, it is possible to say that sternotribic violet species are adapted for solitary bee pollination. However, since all species investigated so far are visited by solitary bees and are therefore to some degree sternotribic, it becomes of interest to discover what aspects of floral biology manipulate pollinators into nototriby and to ask if they are of evolutionary significance. Although no single floral character appears to be responsible for this, it is possible to identify a character complex, or syndrome, which is associated with nototriby. This syndrome does not exclude sternotribic pollinators but lowers the frequency of their visits. Each character may be more or less developed in nototribic violet flowers, but their combined function does effectively "screen out" many or most sternotribic pollinators. For example, in mixed populations of *Viola rostrata* and *V. papilionacea* sternotribic pollinators forage almost exclusively on the latter species.

Characters of the syndrome are listed in Table 2 and illustrated in Figure 4. Items 2 and 3 in Table 2 suggest high sensitivity to nectarguide patterns among nototribic visitors. This has been shown experimentally for butterflies by obscuring or altering color contrasts and guide lines. These insects fail to orient correctly to the corolla-tube and food source when the normal patterns are altered. The significance of the "beards" of hairs (Table 2, item 5) on the lateral petals is chiefly for sternotribic visitors which require them as footholds as they feed from an inverted posture. Item 9 in Table 2 has puzzled many students of *Viola*. The rostellum of many groups of species, especially in the South American

TABLE 2. Characters of nototribic and sternotribic flowers.

Nototribic	Sternotribic
1. Lateral petals overlapping anterior petal to form a composite "landing platform."	Petals various, usually no special association of anterior and lateral petals.
2. Color patterns and contrasts on all petals.	Petals more uniform in color.
3. Posterior petals with nectarguides.	Posterior petals without nectarguides.
4. Posterior petals held erect.	Posterior petals often reflexed.
5. "Beards" of hairs on lateral petals usually absent.	"Beards" present.
6. Nectar spur long and produced into a tube formed by the proximity of the genitalia to the anterior petal; nectar deeply hidden.	Nectar spur short with space between genitalia and anterior petal; nectar not deeply hidden.
7. Anterior petal furrow well developed.	Anterior petal furrow poorly developed or absent.
8. Nectar spur often horizontal or downward-curving.	Nectar spur upward-curving.
9. Style has simple form without a clearly differentiated rostellum.	Style has complex form with a clearly differentiated rostellum.

sections, shows astonishing variation of form with many kinds of bizarre protuberances. It is suggested that their function is to guide the proboscides and heads of sternotribic visitors beneath the rostellum and over the opening of the stigmatic cavity. Tactile guides such as these are required since the eyes of the sternotribic visitor are not in a position to observe the precise location of the passages leading to the nectar (see Fig. 3).

#### FLORAL SYNDROMES AND THE POSSIBILITIES FOR COEVOLUTION

There are a few clear cases of coevolution between flowers and pollinators in *Viola*. For example, the European *V. calcarata* and *V. cornuta* are both extreme nototribes adapted for hawkmoth pollination. Table 3 lists the frequencies of visits of individual insect genera to twelve violet species, and this data tempts speculation. *Viola nuttallii*, *V. eriocarpa*, *V. adunca*, *V. blanda*, and *V. fimbriatula* appear to be almost exclusively pollinated by solitary bees of the genera *Osmia*, *Andrena*, and members of the family Halictidae. The mean tongue-length of these bee visitors is 4–5 mm, and they are all 9.0 mm–10.0 mm in body-length—appropriate dimensions for the size of the flowers of the five violet species. The flowers do not have any clearly differentiated "landing platform," the styles are short with clearly differentiated rostellae, the corolla-tubes are lax, and the bunches of hairs ("beards") on the lateral petals are invariably convenient for the bees to cling to as they feed upside-down.

*Viola striata* appears to be a true generalist with many visits from *Osmia*, *Andrena*, *Halictids*, *Bombus*, and *Rhingia* (Table 3). *Viola papilionacea* is similar with frequent visits from all the above insects plus *Bombylius*. However, if we plot percentage pollination against the percentage of sternotribic visits for *V. striata* and *V. papilionacea* (Fig. 5), it appears that the former is relatively unaffected by an increase in nototribic visits, while the latter clearly experiences a drop in pollination as nototriby increases. The same pattern appears when

TABLE 3. Frequency of visits by individual genera of insects to each of twelve species of *Viola*; expressed as a percentage of the total number of visits taken from five populations of each species.

Visitor Species	Viola Species											
	<i>nuttallii</i>	<i>eriocarpa</i>	<i>striata</i>	<i>reichenbachiana</i>	<i>rostrata</i>	<i>hirta</i>	<i>adunca</i>	<i>blanda</i>	<i>papilionacea</i>	<i>fimbriatula</i>	<i>pedata</i>	<i>tricolor</i>
<i>Osmia</i>	49	9	11	0	5	27	72	5	16	53	0	?
<i>Andrena</i>	25	53	17	0	4	0	0	59	19	0	63	?
Other solitary bees	10	23	22	3	19	13	17	23	29	42	1	?
<i>Bombus</i>	0	0	19	19	.5	40	0	0	5	5	10	?
<i>Rhingia</i>	0	7	23	3	10	0	0	7	13	0	4	?
<i>Bombylius</i>	1	6	1	8	55	20	5.5	5	12	0	1	?
Lepidoptera	12	1	2	0	1.5	0	0	0	2	0	21	?
Other insects	3	1	5	67	5	0	5.5	1	4	0	0	?



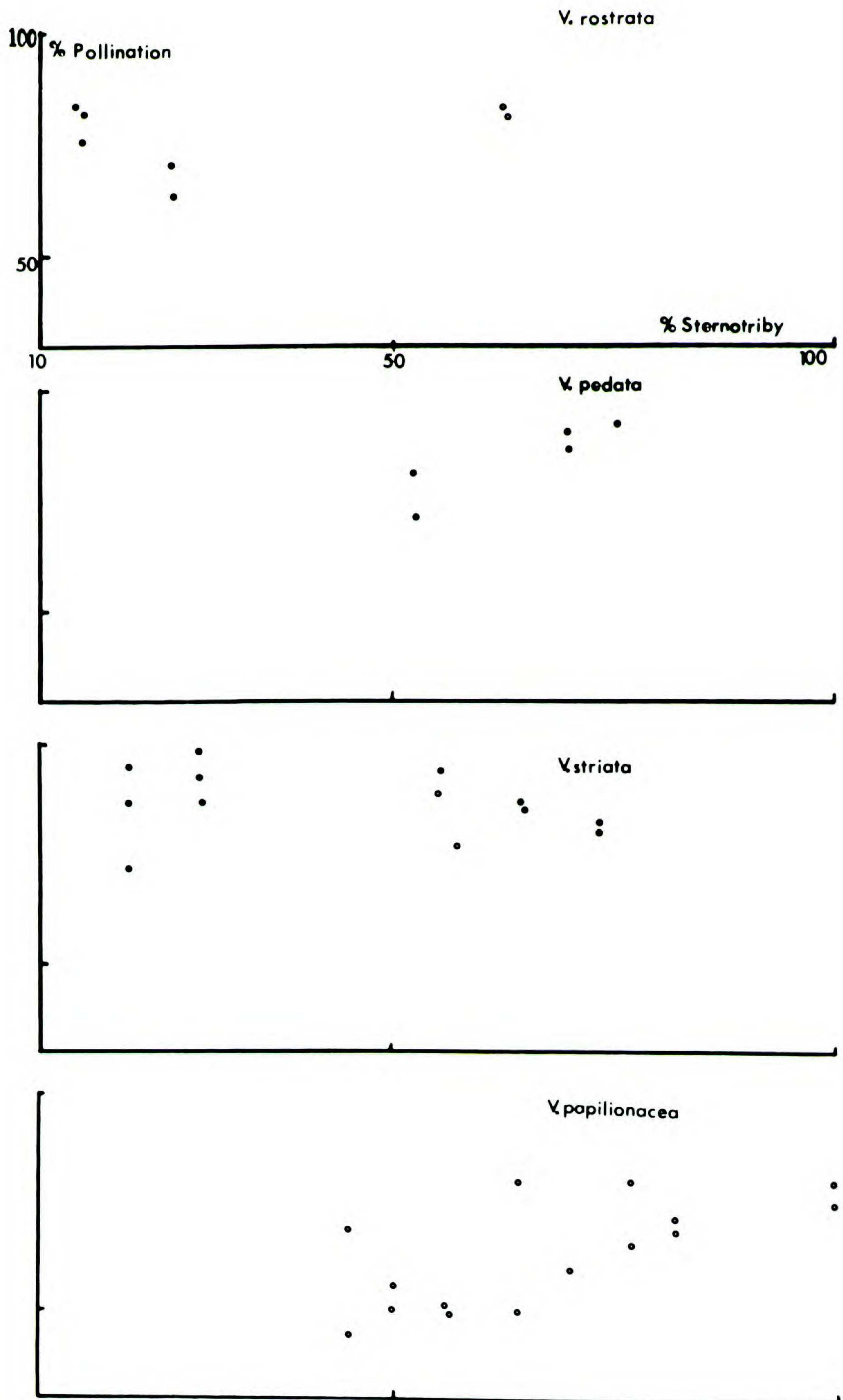
percentage seed-set is plotted against percentage sternotriby (not shown). This is evidence that *V. striata* is a true generalist being adapted to broad-spectrum pollination while, by contrast, *V. papilionacea* is not.

It is possible that because of its close resemblance to solitary bee-adapted species *Viola papilionacea* was once primarily pollinated by these insects. It still is in some habitats. However, today, probably as a result of several hundred years of habitat disturbance by man, its populations occur throughout a great variety of habitats including roadsides, backyards, and waste ground where prolific cleistogamous seed production and vegetative propagation enable it to spread like a weed. Many of its populations experience low frequencies of sternotribic pollination (Fig. 5) and highly variable pollinator "climates." At the same time its flowers show a remarkable degree of polymorphism, and it is tempting to suggest that the original floral syndrome is disintegrating in many habitats and the new morphs are being favored by different groups of pollinators in a process of disruptive selection. This is detected by a reduction in percentage pollination.

The nototribic species show adaptive radiation to special groups of pollinators. *Viola reichenbachiana* is pollinated chiefly by small syrphids and butterflies and may be coevolving with them towards complete nototriby. *Viola rostrata* is pollinated chiefly by *Bombylius* to which its flower is well adapted. The flowers of these species have a landing platform (poorly developed in *V. rostrata* because *Bombylius* hovers while feeding), bands of color contrast near the mouth of the corolla-tube, attenuated styles with simple rostellae, long petal-spurs, and deeply hidden nectar. When percentage pollination is plotted against percentage sternotriby for *V. rostrata* (Fig. 5), there is little variation in pollination efficiency. When the frequency of nototribic visits approaches 100%, pollination remains high, and it is reasonable to assume that the particular floral morphology of *V. rostrata* is the product of coevolution with the nototribic *Bombylius*. *Viola pedata*, on the other hand, appears to be in a position similar to *V. papilionacea* with decreasing pollination correlated with increasing nototriby. *Viola pedata* is apparently still primarily sternotribe, and yet the flowers exhibit many nototribic characters: there is a large landing platform, all petals exhibit color contrasts, the lateral "beards" are absent, the nectar-spur is long and the style, although unique in shape, is simple with no rostellum. The species is visited by nototribic hawkmoths such as the bumblebee mimic *Hemaris* and by large solitary bees. The behavior of these latter insects is particularly instructive; most attempt sternotribic feeding, but species of *Anthophora* and *Synhalonia* are forced to feed *nototribically* to get food. Consequently, we have evidence that *V. pedata* is in transition from sternotriby to nototriby and may experience reduced pollination as a result. The transition is suggested most strongly by the ambivalent responses of solitary bees.

#### PHYLOGENETIC CONSIDERATIONS

There have been several careful phylogenetic studies of the genus *Viola* (e.g. Clausen, 1927, 1929; Gershoy, 1928) with considerable agreement as to which



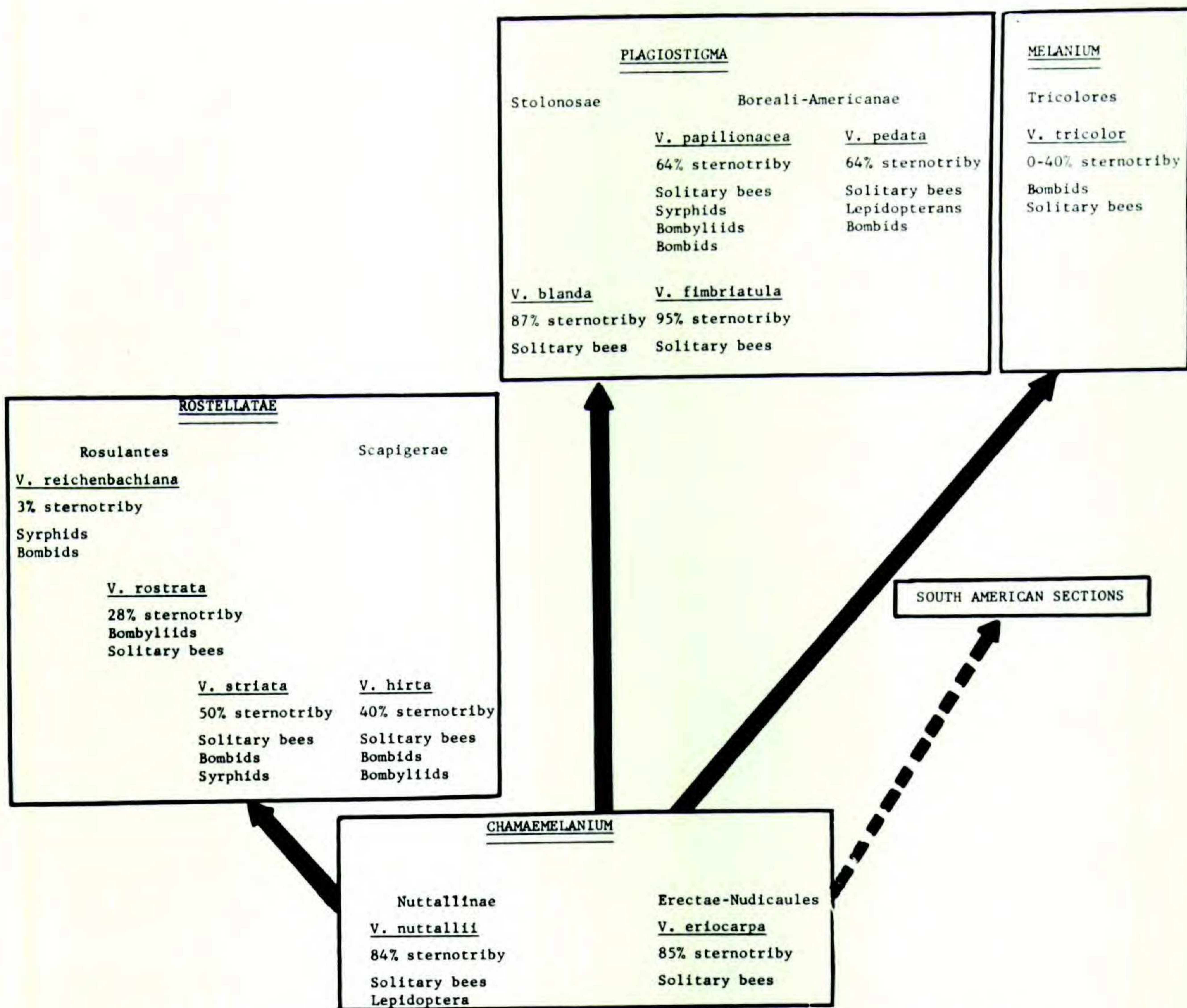


FIGURE 6. A proposed phylogeny of pollination systems in the genus *Viola*.

species are ancient and which are recently evolved. Species of the section *Chamaemelanium* are thought to be the oldest violets, and they are represented in this study by *V. nuttallii* and *V. eriocarpa*. These are yellow-flowered with similar floral morphologies and pollinated by solitary bees. Both species have been found to be approximately 85% sternotribic wherever they have been studied. If we assume this to be the primitive condition for *Viola*, we can trace the evolution of pollination systems through the other sections of the genus (see Fig. 6). Clausen (1927) believed that the section *Rostellatae* to be close to *Chamaemelanium* and derived from it. *Viola adunca* is representative of the Rostellate species closest to the ancestral condition; it exhibits 89% sternotriby. Indeed, Clausen said of this and other closely related species that if they were yellow-flowered they would be very like *Chamaemelanium* violets. The remain-

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FIGURE 5. Percentage pollination and percentage sternotriby for four species of *Viola*. Percentage pollination is the proportion of the total number of ovules in each sample which are matched by the presence of a compatible pollen grain in the stigmatic cavities of the flowers analysed. Percentage sternotriby is the proportion of the total number of insect visits to each sample which were of this type.

ing Rostellate violets studied showed a progressive decrease in sternotriby. *Viola striata* and *V. hirta* with 50% and 40% sternotriby respectively appear to be generalists, while *V. rostrata* (28%) and *V. reichenbachiana* (3%) represent lines of nototribic evolution. All these violets are blue-flowered; and with increasing nototriby there is a reduction or loss of lateral petal hairs, a tendency for the lateral and anterior petals to overlap, and a reduction in the differentiation of the stylar rostellum to produce a simple, non-papillate, terminal stigmatic opening (see Fig. 4).

The section *Plagiostigma* has many obviously sternotribic species such as *Viola blanda* (87%) and *V. fimbriatula* (95%). One suspects that if *V. papilionacea* was not as ecotypically variable as it is and was more restricted with respect to habitat—like *V. fimbriatula*—it would exhibit a higher degree of sternotriby than 64%. *Viola papilionacea* and *V. pedata* may represent early transitional stages from sternotriby to nototriby, suggesting (when considered with *V. rostrata* and *V. reichenbachiana*) parallel evolutionary trends in the sections *Plagiostigma* and *Rostellatae*. The *Melanium* violets are mostly nototribically pollinated by bumblebees, butterflies, and moths. *Viola tricolor* exhibits a nototribe floral syndrome and may be sufficiently representative of the section to suggest an early and direct evolution towards nototribic pollination (see Fig. 6).

#### THE PROCESS OF DIFFERENTIATION IN THE EVOLUTION OF POLLINATION SYSTEMS

The dual sets of stimuli presented by the *Viola* flower elicit both sternotribic and nototribic types of response. These provide a broad base of variation available for selection, which, as in the case of trends towards nototriby, may be sufficiently intense for the production of distinct floral syndromes. The field data suggest processes whereby new pollination systems may differentiate, by selection, from pre-existing systems. Furthermore, within the several hundred extant violet species we have the opportunity to examine an array of intermediate stages in the greatest detail. From the considerable adaptive radiation it is possible to build up a conjectural picture of possible steps in the evolution of violet pollination systems.

Selection sometimes operates by the gradual accumulation of floral characters more favorable to one group than another. This may be detected by a drop in pollination efficiency but does not necessitate complete discontinuities in pollination, either in time or space. Adaptive radiation may occur, perhaps originating with a generalist floral syndrome, in response to differential pollinator complexes, throughout a large geographic area.

The generalist syndrome may have had a special significance for *Viola*: the visitor species lists accumulated for North America closely resemble those of other workers (mostly unpublished) from Europe and parts of Asia. The pollinator complex of *Osmia/Andrena/Halictids/Bombus/Rhingia/Bombylius* and various Lepidoptera is apparently available to violet populations over a vast geographic area of the north temperate zone. Many violet populations receive

visits from most of these insects (see Tables 1 and 3), and many floral morphologies permit some pollination as a result of their feeding activities (Beattie, 1971). Therefore, the basic floral structure is more or less adapted to a pollinator complex which has a wide geographic distribution. This being so, it is not surprising to find that the basic structure remains identical among the 350–400 known species—a violet flower is instantly recognisable despite enormous differences in vegetative structure such as vines, succulents and shrubs—and that variation is limited to detailed structure, presumably as a result of coevolution with particular groups of pollinators. This pattern of variation may have been of special adaptive significance during two major migrations of the genus in the northern temperate zones: First, outwards from its putative center of origin in the Central and South American, sub-tropical and tropical montane environments and second, from the southern-most limits of the final glaciation back to its contemporary northern-most limit of distribution.

It is interesting that adaptive radiation in the north temperate regions has exploited so many facets of the potential pollinator complex with so little change in reproductive structure. This may reflect a general paucity of pollen vectors in this region as compared to the tropics. Thus, the genus has radiated at comparatively little genetic and energetic “expense” and may also, therefore, maintain the option of reverse evolution should general shifts of pollinator climates occur. By contrast similar radiation among tropical plant groups, *e.g.* the *Bignoniaceae*, have required major reorganisations of floral structure accompanied by a higher frequency of specialisation of pollination systems.

In conclusion it seems that for many plant species the minority and majority pollinators are of equal interest, for together they constitute the variation available for selection of novel floral structures. By understanding their impact upon reproductive success, and by measuring it, we gain some insight into the processes whereby pollination systems evolve.

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